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The benthic litter habitat with its sediments load in the inundation forest of the Central Amazonian blackwater river Tarumã Mirím

by

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Abstract

Submerged leaf litter is the principal habitat of the aquatic fauna in nutrient-poor, acid streams and rivers of Central Amazonia and their inundation forests. To estimate the magnitude of this habitat, the number of leaves per area and their mean size and dry weight were determined at various sampling stations in the different flooded forests along the Tarumã Mirím River and its headwater streams. Samples were collected from the irregularly inundated stream valley bottoms (baixios) of the headwater streams through the igapó, which is subject to annual immersion and emersion phases. On these occasions, I noted a heavy load of sediments which covered the leaf litter after the water had receded. The sediment quantity per unit area in this habitat increased with the duration of the inundation phase and reached several tons per hectare annually in the igapó (inundation forest). These deposits include three major components: sand, clay and organic particles (fine detritus). The possible origin of these components is briefly considered: There are demonstrable reasons why these substantial sediment quantities have hitherto escaped observation.

Keywords: **Leaf litter, river sediments, inundation forest, Central Amazon, Brazil.**

Resumo

Nas águas pobres e ácidas da Amazônia Central a serrapilheira submersa é o principal habitat da fauna aquática. Para estimar a ordem de grandeza deste habitat, foram determinados o tamanho (cm^2/folha), o peso seco das folhas e o número de folhas por área em várias posições da floresta ao longo do Rio Tarumã Mirím, a partir das cabeceiras e seus baixios, atravessando o igapó anualmente inundado, até o igapó baixo na área da boca do rio ("ria-lake"). Nesta ocasião notou-se uma carga considerável de sedimentos cobrindo as folhas imediatemente apos a retirada das águas no período do vazante (agosto-setembro). A área foliar diminui de 75 cm^2 nos baixios das cabeceiras até 20 cm^2 na área do "ria-lake"; o número de folhas/m^2 variou de 671 a 919, com exceção da área do "ria-lake", onde constatou-se 409/m^2. Portanto, o peso seco da liteira de 7.5 t/ha nos baixios cai até 0.6 t/ha na área do "ria-lake". O peso seco dos sedimentos foi estimado em 1 - 2 t/ha · ano por metro de profundidade d'água na cheia máxima (Junho).

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Introduction

The Tarumã Mirím is one of the innumerable small, meandering rivers that drain the Central Amazonian lowland. Like all tributaries of the Amazon and the Rio Negro in this region, its lower course lies in the zone of the annually flooded inundation forest (igapó), while its headwaters originate in short and relatively steep valleys, which descend from the plateau, circa 60 to 120 m above sea level, into wide, completely truncated river valleys with hydromorphic soils. These stream valley bottoms (baixios) are irregularly flooded by heavy rains between January and June, and they contain numerous, more or less permanent water holes and ponds. The streams are either transparent and colourless (clear water), or, owing to a high content of humic substances, transparent orange-brown (black water), depending on whether they drain dense clay soils (latossols) or sandy podsols, respectively (SIOLI 1954, 1975, 1984; KLINGE 1966; LEENHEER 1980; CHAUVEL et al. 1987). The nutrient poverty (electric conductivity = 7 - 30 $\mu S_{20}/cm$) of these acid (pH = 3.8 - 5.8) waters (WALKER 1988; ANONYMUS 1972; SCHMIDT 1972) precludes growth of phytoplankton and of aquatic macrophytes, in contrast to the richer waters of the Solimões/Amazonas (FITTKAU et al. 1975; SIOLI 1984). The fauna of these poor waters is sustained by allochthonous input from the forest, such as leaf litter, dead wood and fruits. Submerged litter with its saprophytic, decomposing fungi is not only the first link in the food chains supporting the aquatic fauna (FITTKAU & KLINGE 1973; WALKER 1985, 1987), but also the site of protective niches for the larger consumers. The fauna is therefore predominantly benthic and concentrates in the submerged litter. During the low water period, from September or October to January or February, when the river is confined to its bed, the density of these larger organisms in submerged litter beds can reach several hundred individuals per square meter. This includes fish, shrimps and larger insects, excluding chironomids (HENDERSON & WALKER 1986, 1990). As water levels rise ("enchente", January to June) this fauna spreads to the igapó. As this is also the period of reproduction, shrimps, for example, maintain a density of about 12 individuals per square meter despite the continuous expansion of the aquatic habitat (WALKER & FERREIRA 1985), and single, submerged litter leaves carry, on the average, 10 - 20 chironomid larvae (WALKER 1988; unpublished data).

To complement faunal studies, the litter habitat exposed by the receding river waters was repeatedly sampled. On these occasions, I observed a substantial layer of fine sediments on the emerged litter leaves. Since blackwater streams like the Tarumã Mirím are thought to be poor in suspended sediments (BRINKMANN 1986; LEENHEER & DE MENEZES-SANTOS 1980), I decided to examine these sediments along with the other material collected. The results suggest that sediment deposition in blackwater inundation forests may be more important than generally assumed.

Study area, material and methods

1. Study area

The approximate collection sites, Sampling Stations 1 to 9, are indicated on the map in Fig. 1. Station 4 is accessible by a 40 minute walk from the Igarapé Pau Rosa, all other Stations are accessible only by some rather difficult canoe navigation. The headwater region and the middle reaches of the river down to Station 7 lie under a closed, high canopy primary forest. Further downriver, the forest diminishes gradually in height and species richness, as prolonged, annual inundations increase the physiological stress on germination and growth. Five families, subsisting on fish and small manioc plantations, live between Stations 6 and 8; deforestation along the river does, however, not exceed 50 to 100 m per family. Further downstream the human population is somewhat more abundant. However, these small farms are generally situated on the terra firme (= upland) above the inundation levels. The only significant deforestation of the inundation forest itself occurred below Station 9, which lies in more open vegetation on compact clay soil with patches of dense saplings beside areas of few large trees and frequent tree falls. While the water level is low, the river is flanked by steep vertical banks, about 0.8 to 1.5 m in height. The highest water levels are reached in June, when the water depth above the forest floor is circa 2 to 3 m at Stations 5 and 6, and 3.5 to 5 m at Station 7, about 6 m at Station 8, and 7 to 11 m at Station 9. Data from multiple collections during the years 1978 to 1990 are available from Stations 7 and 9 only. In 1986 the water did not recede from the lower parts of the igapó. Thus, Station 9 remained under water from January 1986 to October 1987. The average declivity of the river is about 0.4 m/km measured on a straight line without considering meanders, which, during low water levels, leads to a mean water flow of 12 to 40 m/minute, depending on topography and rainfall. In the valley of the head water streams at Stations 1 to 4, inundations due to exceptionally heavy rains may reach over 1 m in depth, as determined from observation of litter leaves and debris stuck to the upriver side of tree trunks.

All the material reported on was collected on the forest floor of the igapó (Stations 5 to 9), of the irregularly inundated stream valley bottoms (baixios) and of the ponds located along the headwater streams (Stations 1 to 4). The litter habitat of the stream and river beds has not yet been sampled.

2. Material collected

The objective was to characterize the litter habitat of the aquatic mesofauna that adheres to single leaves (WALKER 1988) and that of the macrofauna that lives in the loose litter layer. I did not intend to determine the total amount of organic substrate on the forest floor, as did IRMLER (1975) downstream from Station 9. Depending on species, submerged litter leaves may remain superficially intact for many months before they rather suddenly break up (JUNK & HOWARD-WILLIAMS 1984; WALKER & DINIZ in prep.). The lower layer of the fragmented litter is less attractive for the benthic fauna and has not yet been sampled.

Litter leaves range from a few mm (Mimosaceae) to several meters (palms) in length. What strikes the eye, though, is an average sized litter, which covers the forest floor more or less evenly. The leaves examined were collected from this average sized litter and ranged from circa 4 to 30 cm in length.

Dead wood collected did not include branches longer than the diagonal of the sampling quadrate (70 cm), and most pieces were considerably shorter.

The sediments deposited on the litter leaves were noted only when sampling began in August 1987. The decision to collect these fine deposits was made in the laboratory, when the leaves had to be washed to determine their surface area and dry weight. These deposits consist of three major components: fine silica sand, clay and dark, brown, organic detritus, which, as seen under 10x magnification, includes fecal pellets, bits of plant tissues and smaller, unidentifiable particles.

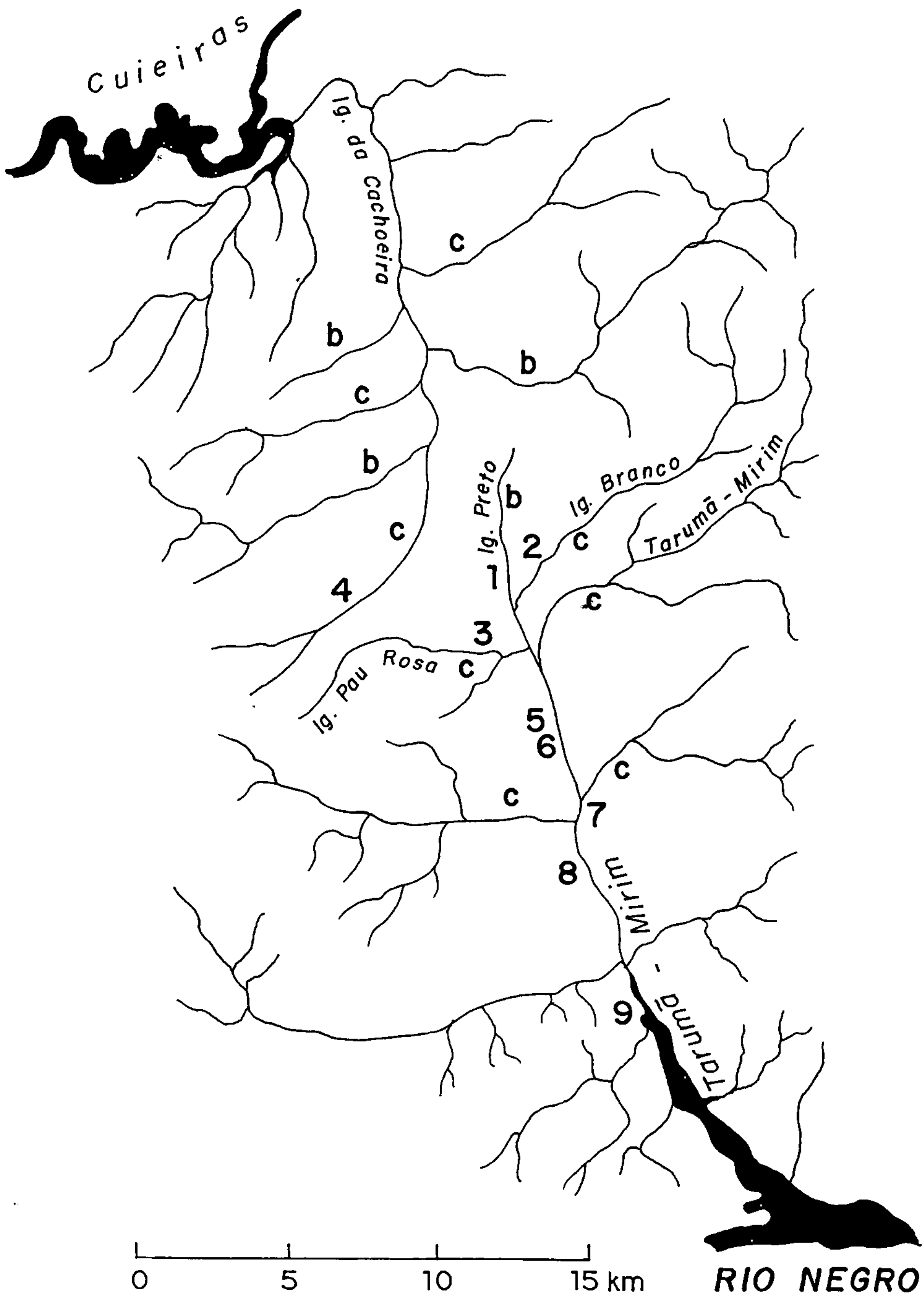

Fig. 1:
The Tarumã Mirím River, which flows into the Rio Negro circa 20 km West of Manaus, and the stream Igarapé da Cachoeira, with the approximate position of the nine sampling sites (Stations 1 to 9 in Tables 1 to 3 and in the text). c, b, for clear and blackwater tributaries respectively, as determined during excursions between 1984 and 1988.

3. Methods

For the analysis of the litter layer, 4 to 6 quadrates of 50 cm x 50 cm were laid out at intervals of 5 m along a straight line along the edge of the receding water, 12 to 36 hours after emersion during the period of falling water levels (vazante). Major impediments such as fallen trees, large branches, shrubs etc, were avoided. All leaves with more than about 50 % of their surfaces intact were counted and collected from each quadrate. Wood fragments were collected in different bags. In the laboratory, the leaves were carefully washed, dried at 70 to 90 °C and weighed. Wood was dried until the weight stabilized. The washing water of the leaves was filtered through Whatman paper filters of predetermined weight, and the filters with their sediments were dried and weighed. By subtraction of the respective filter weight, the sediment charge on an area of 0.25 m^2 was calculated. These determinations do not include the sediments deposited on the leaf fragments that were not collected, nor, of course, the sediments that had drifted through the litter layer onto the forest soil; thus, the total weight of the sediment deposited per 0.25 m^2 area during one inundation period must be greater than the corresponding value in Table 2.

On some occasions, the sediment load of individual leaves still submerged in ponds (Stations 1 to 4) and of inundated live vegetation in the igapó (Stations 5 to 7) was determined. Randomly chosen, entire leaves were carefully lifted out of the water; nevertheless, some of the lighter particles were invariably swept off the leaf. Leaves and sediments were then dried and weighed in the laboratory. To estimate the litter layer in the baixios, quadrates were set in random locations in the depressions at the edge of ponds. Strong currents during flooding after heavy rains sweep the elevated positions occasionally almost clear of litter.

To establish leaf size, individual leaves were collected randomly while blindfolded, either in the sampling areas in the field or from the litter samples in the laboratory. Incomplete leaves were discarded.

Litter depth was determined by driving a spike through the litter into the ground and counting the number of leaves pierced (3 spikes per quadrate).

Results and conclusions

The results are summarized in Tables 1 to 3. For comparison, the results will be averaged for each of the three distinct regions: First, Stations 1 to 4 in the baixios, the stream valley bottoms of the terra firme, which are occasionally flooded by heavy rains and include water holes and ponds; second, Stations 5 to 8 in the middle igapó with regular, annual immersion and emersion phases; and third, Station 9 in the lower igapó with irregular emersion phases, and which remained inundated from January 1986 to October 1987.

The data permit the following conclusions:

1. Leaf litter

Leaf number/0,25 m^2 is similar in the baixios and the middle igapó ($P \cong 0.5$; χ^2-test), but far fewer leaves accumulate in the lower igapó ($P < 0.01$). Mean leaf surface (cm^2/leaf) however, diminishes from the baixios to the middle igapó ($P < 0.005$; t-test), and from there to the lower igapó ($P < 0.01$).

The product of leaf number per quadrate and leaf size provides an estimate for the total litter area per quadrate that is available for colonization by the benthic fauna. These values are different in the three areas and read: 1.4609 m^2 in the baixios, 0.8369 m^2 in the middle igapó ($P < 0.01$; t-test) and 0.2073 m^2 in the lower igapó ($P < 0.025$ for the two igapó regions). These values are not representative for the forest of the baixios as a whole, because the quadrates were set in the depressions, where litter and water accumulates. Still, working in these areas, one gets the impression that the baixios

Tab. 1: Mean size (cm^2) and dry weight (g) of litter leaves from various sampling stations (Fig. 1), converted to dry weight per 100 cm^2 of leaf area. $\bar{x}$ = mean, $\bar{\bar{x}}$ = mean of means; SD = standard deviation; n = number of samples assessed.

Sampling station & Sampling date	Leaf litter Size (cm^2) $\bar{x}$ / * $\bar{\bar{x}}$	± SD / ± SD	(n)	Weight (g) $\bar{x}$ / * $\bar{\bar{x}}$	± SD / ± SD	(n)	=>g/100 cm^2
1 May 9, 88	67.55	±21.65	(20)	0.775	±0.327	(20)	1.147
1 Jun 7, 89	76.70	±29.00	(10)	0.974	±0.103	(10)	1.269
2 May 5, 88	76.52	±38.69	(23)	1.040	±0.740	(23)	1.359
2 Jun 8, 89	81.50	±48.40	(10)	1.044	±0.128	(10)	1.281
6 Aug 26, 87	38.00	±19.86	(31)	0.421	±0.016	(31)	1.108
6 Mar 1, 89	40.65	±20.66	(20)	0.485	±0.260	(18)	1.193
7 Mar 1, 89	* 47.96	±10.96	(2x15)	* 0.563	±0.023	(2x15)	1.174
7 Apr 20, 89				* 0.538	±0.199	(5x5)	
9 Oct 2, 87	20.26	±12.78	(23)	0.145	±0.364	(23)	0.716

are richer in litter than the middle reaches of the igapó. For the two igapó regions, however, the values seem to be representative. Thus, we find that total leaf area in the middle igapó (0.8369 m^2) is three to four times larger than the area covered by the respective leaves (o.25 m^2); this value is confirmed by the independently taken spike samples, which showed a mean litter depth of 3.67 leaf layers (range 2 to 6; 45 samples). In the lower igapó, the total leaf area is smaller than the sampling quadrate. Bare clay soil is indeed a characteristic feature of this region.

That the difference in litter richness is paralleled by a difference in benthic animal biomass is suggested by comparing IRMLER's (1975) estimate for the lower igapó below Station 9 of 0.28 g/m^2 fresh weight, and a minimum estimate for the middle igapó of circa 2.5 g/m^2 (WALKER 1988). A more critical assessment must await the evaluation of several years' sampling.

There is no difference in leaf weight/100 cm^2 leaf area between the baixios and the middle igapó; however, leaves are lighter in the lower igapó ($P < 0.025$; t-test). This may be due to the prolongued 17 months inundation period. However, the weight of the freshly shed leaves would have to be known to support this suggestion. Annual litter production is 5 to 7 t/ha (cf. ADIS et al. 1979; FRANKEN et al. 1979) and leaf fall occurs mainly during the dry season between August and December and hence, during the emersion phase. For the middle igapó this means that circa 40 % of the annual litter production fractionate during the immersion phase from February to September. This value is roughly similar to those obtained in independent experiments on underwater decomposition, in which about 30 % of the leaves fractionate in eight months (WALKER & DINIZ in prep.).

2. Sediments

The surprise came with the heavy load of sediments on the loose litter in the middle igapó, which amounts to roughly 3 to 8 t/ha · year. Sediment weight seems to be correlated with the period of inundation. Thus, Station 5 was still partially inundated in September 1989, while in September of the previous two years the water had already retreated from Station 8, which lies at least 7 km further downriver (not considering meanders). The samples from September are heavier than those from August 1987 and 1988 at Station 6 (Table 2, $P < 0.01$; t-test). The scarcity and brittleness of the leaves in the lower igapó preclude comparative estimates of Station 9, however, considering the data from further upriver (Stations 5 to 8) one would expect more than 10 t/ha · year in the lower igapó.

Flooding of the baixios (Stations 1 to 4) during the rainy season is obviously also accompanied by a sedimentation process. The limitation of the sampling to pools and depressions does, however, not allow for large-scale comparison. Although the results from the middle igapó (Stations 5 to 8) are conclusive in themselves, more generalized conclusions will be possible only after extended quantitative sampling of sediments.

Table 3 answers the question, why these substantial sediment quantities had not been previously observed. The top layer of leaves actually submersed (Stations 1 and 7) carry only 0.26 g/100 cm^2 of leaf surface. After drying, this looks like a thin, insignificant film, as also noted by IRMLER (1976). Moreover, the water recedes during the dry season, when new litter is shed, thus masking the conditions resulting from the immersion phase. In addition, afternoon rains are frequent, even during the dry period, and a single rain washes the leaves of the top layer clean. During the inundation phase, sediments seem to drift downward, as would be expected as a result of currents and animal activity; hence, the lower-level leaves carry more sediment. Upon drying, leaves and sediments transform into a compact soil layer, which is quickly covered by new litter fall. These conditions, together with the poverty of suspended particles in black water, lead to the conclusion that sedimentation in blackwater inundation forests is insignificant. Yet, one can argue that black water is poor in suspended particles because the rate of sedimentation matches the rate of suspension, hence, sediments accumulate on the inundated forest floor and not in the water column.

From the topography of the region, one would certainly expect sedimentation in the flood plains of the igapó and erosion in the area of the headwaters. Although there is little run-off and erosion over the slopes of the stream valleys (NORTCLIFF et al. 1979), there is internal particle transport into the valleys as a result of pedogenetic processes (CHAUVEL et al. 1987). These processes result in a mosaic of podsols and latosols along the headwaters and the deposition of silica and clay particles in the stream valley bottoms.

Tab. 2: Dry weight (g) of wood, leaves and of sediments deposited on these leaves per 0.25 m^2 quadrate. Nos = mean number of leaves per quadrate. The maximum water depth in the igapó (Stations 5 - 9) is reached in June; ! the highest water level in June 1989 was circa 2 m above the average of previous years; +) as calculated from the sediment charge on individual leaves in pools along terra firme streams, t/ha is merely given for comparison; ++) see text p. 147. Other symbols as in Table 1.

Sampling station & Sampling date Water depth in June	Leaves Nos/0.25 m² x̄	± SD	(n)	g/0.25 m² x̄	± SD	(n)	t/ha	Wood g/0.25 m² x̄	± SD	(n)	t/ha	Sediment g/0.25 m² x̄	± SD	(n)	t/ha
1 June 7, 89	195.0	±62.0	(4)	185.13	±76.78	(4)	7.40					+) 40.36	~50%	(4)	(1.61)
2 0.5 - 1.5 m	191.8	±15.7	(4)	196.46	±14.34	(4)	7.58					+) 61.31	~50%	(4)	(2.45)
5 Sept. 8, 89 ~ 2.6 m !	167.9	±29.4	(4)	88.44	±12.28	(4)	3.54	66.1		(1)	2.64	170.10	±103.04	(4)	6.80
6 Aug. 26, 87 ~ 2.5 m	210.2	±122.9	(10)	79.03	±28.10	(10)	3.16	101.47	±64.30	(4)	4.06	112.04	±53.55	(10)	4.48
Aug. 25, 88 ~ 2.5 m	188.5	±99.3	(4)	108.49	±51.71	(4)	4.34	63.77	±44.19	(4)	2.55	81.05	±21.75	(4)	3.24
8 Sept. 17, 87 ~ 6 m	229.8	±77.5	(6)	73.2	±34.79	(6)	2.93	120.16	±146.47	(6)	4.81	204.45	±96.58	(6)	8.18
9 Oct. 2, 87 ~ 9m	102.3	±86.0	(10)	15.04	±14.39	(10)	0.60	71.70	±58.73	(10)	2.87				++) > 10.0 ?

3. The origin of the sediments

There are no coherent investigations of the origin of sediments in Amazonian black waters, but miscellaneous observations allow for the following considerations.

The water level in the igapó rises during the rainy season, when the streams flood their valleys, and when water volume and flow velocity are at their maximum. Blackwater streams draining sandy soils sweep sand downstream, while clear streams draining clay soils carry a substantial load of lamellar clay particles, as visible from a marked Tyndall effect (particle reflecting light). Both carry organic particles, mainly feces of chironomids and oligochaetes, as well as larger items, such as plant debris and forest litter. For instance, 70 ml bottles, suspended for three days in the water column of the Igarapé da Cachoeira during heavy rains collected, on the average, 2 ml of fine suspended detritus (WALKER 1985).

Tab. 3: A. Sediment charge per leaf area of submerged litter in the stream valley bottoms (baixios, Station 1 to 4). Brackets: mean leaf size in the area determined on other occations. B. Mean sediment charge on top and lower layer leaves, and the effect of rain clearing the top layer leaves of sediments. +) This independent calculation of g sediment/leaf x number leaves/0.25 m² yields a similar weight/ha value as those shown in Table 2. Other symbols as in Table 1 and 2.

	Sampling station & Sampling date	leaf area cm²/leaf	Sediment, g/leaf x̄, / * x̄,	± SD, / ± SD,	(n) / (n)	= g/100cm²	Observations, water quality, water depth (cm)
A	1 Ig. Preto June 7, 89	76.7	* 0.207	±0.097	(4x10)	0.269	black water pools in baixio 10 - 25 cm
	2 Ig. Branco June 8, 89	81.5	* 0.321	±0.170	(4x10)	0.394	Clear water pools in baixio 10 - 25 cm
	3 Ig. Pau Rosa July 1, 89	(79.0)	* 0.613	±0.237	(2x10)	0.776	"
2	4 Ig. da Cachoeira July 1, 89	(79.0)	0.343		(1x10)	0.434	"
B	7 Tarumã-Mirím Sept. 26, 89	(59.0)	* 0.154	±0.087	(2x10)	0.261	Mixed water, Top layer leaves ~15 cm, Igapó
	6 Tarumã-Mirím Sept. 26, 89	(40.7)	* 0.015	±0.014	(2x10)	0.037	0 cm; Igapó emersion 25.09.89 after rain
	6 Tarumã-Mirím Sept. 26, 89	"	* 0.468	±0.063	(2x10)	1.150 (~3.73 t/ha) +)	deeper leaves Station 6 see Table 2

The mixing of clear and black water results in complexing between clay particles and humic substances in solution, and in their precipitation under acid conditions (LEENHEER & DE MENEZES-SANTOS 1980). As the Tarumã Mirím is an acidwater river, every tributary contributes to this process.

A further fraction of organic detritus is produced in the igapó during the immersion period. There is the metabolic waste of the organisms that reside in the soil litter and that adhere to the submerged, live vegetation. BRINKMANN (1986) discusses flocculation of colloids in the igapó, and recently it was shown (MANN 1988) that submersed plants, while still alive and in their early stages of decomposition, release dissolved, organic matter, which precipitates on the surface of the vegetation. The live, immersed tree leaves in the igapó certainly carry deposits of organic matter, which consists of a gelatinous substance and of brown detritus particles. For example, groups of five live, green leaves, collected in two sites near Station 6 at 15 to 25 cm and 40 to 60 cm depths, carried a sediment load of 0.07 g and 0.12 g (dry weight), which corresponds to 0.025 and 0.042 g/100 cm^2 of leaf surface. At the time of collections, this vegetation had beeen under water for 8 to 10 weeks. These few samples cannot be taken as an average for larger areas, they merely suggest the magnitude of the process. During the latest stages of inundation, the litter in the then shallow igapó is often covered by a thick layer of gelatinous matter, as also noted by IRMLER (1975).

These observations, together with the data in Tables 2 and 3, suggest that sediment production and deposition in the igapó may be of importance for its associated flora and fauna and for regional nutrient cycling. Therefore, limnological and chemical investigation of sedimentation in Amazonian blackwater inundation forests is clearly needed.

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